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SOME NOTES ON THE DEVELOPMENT AND REGULATION OF HEAT AMONG GALLERIA LARVAE

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INTRODUCTION

In carrying on some experimental work on the genetics of the wax moth, **Galleria mellonella** L. (Smith '38), it was noted that the growing larval stages developed appreciable amounts of heat--enough that upon examining on cold mornings in the winter time, the culture bottles were surprisingly warm, having temperatures up to over 40 degrees C. It was thought at first that the heat produced might perhaps be due to some fermentative process going on in the food. This possibility was ruled out since the food, which is dry, honeyless bee combs, (Smith '37) contains neither sugar nor moisture and thus does not "heat". The observations and measurements of the temperatures were made on larvae--the stage during which much heat is developed.

THE PRODUCTION OF HEAT

When it was observed that considerable heat was being generated in the larval cultures, it, of course, aroused some curiosity. Since the organism is a "cold-blooded" animal this pronounced heat production seemed to warrant further investigation. So far as the writer can ascertain, there is only one other case recorded of cold-blooded animals, either among the invertebrates or the vertebrates having the power to raise their own temperature or the temperature of their environment to an appreciable degree. This case is the honey bee, **Apis**, upon which definite measurements have been made by Phillips and Demuth ('14), and others. Bodenheimer ('34), Wigglesworth ('39) and others have reported a number of insects which have a very limited power of both temperature production and regulation. They indicate that this is chiefly accomplished by metabolism and heliotropistic reactions, and by evaporation, respectively.

EXPERIMENTAL

When it was first noticed that the larval stages of **Galleria mellonella** were developing considerable heat, several measurements of the temperature were made by placing the bulb of an ordinary mercury thermometer in the midst of the colony and observing its registrations. In most of these cases the temperature in the colony registered from 10° to 15°C. above the room or incubator temperature. In one case of a large colony of well-fed full-grown larvae among some cultures which were being carried at room temperature (the room temperature ranged around 20° to 23°C.), the temperature of the colony was slightly over 40°C.-- a difference of some 17° to 20°C. This striking heat producing characteristic was investigated still further.

The following is a series of readings of the progressive temperatures of typical room incubated cultures, and of cultures reared in an incubator maintained at 30°C. Culture no. 13/4H14--brother-sister mating, was made on August 12. The room temperatures ranged from about 22°C. during the night, up to around 26°C. during the day time. The pair mated and the female deposited many eggs during the following night. On August 23 the larvae began to hatch and scurry about over the food. From then on the following data were collected:

Table I

Date		Temperature in degrees Centigrade		
		Room	Culture	Difference
August 23	9:30 a.m.	25.5	25.5	0
August 31	4:00 p.m.	26	26.5	.5
Sept. 5	9:30 a.m.	24.5	26.5	2
Sept. 10	9:30 a.m.	25	28	3
Sept. 15	9:30 a.m.	24	27	3
Sept. 20	9:30 a.m.	24.5	29	4.5
Sept. 25	9:30 a.m.	24	30.5	6.5
Sept. 30	9:30 a.m.	24	33	9
Oct. 5	9:30 a.m.	23.5	32.5	9
Oct. 10	9:30 a.m.	23.5	37	13.5
Oct. 15	9:30 a.m.	24.5	38.5	16
Oct. 20	9:30 a.m.	23	33	10
Oct. 25	9:30 a.m.	23	29	6
Oct. 30	9:30 a.m.	23.5	26	2.5
Nov. 5	9:30 a.m.	23.5	24.5	1
Nov. 10	9:30 a.m.	23	23.5	.5
Nov. 15	9:30 a.m.	23.5	24	.5

Some adults began to emerge on October 25. However, there were some larvae which had not yet reached the comparatively quiescent pre-pupal and pupal stages. It will be noted that there is a gradual rise in temperature as the larvae increase in age and size and a more sudden decrease as they begin pupating. This is to be expected on the basis of the gradual increase in size of each growing mass (some definite figures will be given later) and the relatively shorter time required to go into pupation after the last larval stadium.

It should be remembered that the temperature of the growing culture would have been greatly in excess of that shown here had there been some means of preventing the constant radiation of heat away from the culture. The amount of heat that was lost could not be measured by the apparatus at hand.

In the case of either room or incubator cultured larvae, the individuals have a method of regulating the temperature of the colony as a whole, and indirectly, their own individual temperatures. If the temperature gets above 40°C. the larvae scatter themselves about over the surface of the combs and the sides of the culture bottle. In this way the individuals lose considerable heat. When they return to a place within the colony, they tend to reduce its temperature accordingly. They are constantly generating heat, the source of which is interpreted as arising from (a) their constant and rather vigorous muscular activity and (b) the oxidation of relatively large quantities of food as is evidenced by the amount consumed and by their rapid larval growth.

An attempt was made to ascertain this critical maximum temperature of the colony. Repeated measurements of the temperature of room or incubator grown colonies indicated that the highest temperature reached (and this is typical for colonies of full-grown, last stadia larvae) was generally around 39 to 41°C. For a more critical test 160 last stadia larvae were cooled to 15°C. and placed in a pint thermos bottle of standard design with finely broken pieces of food. The food was broken into small pieces so that larvae could penetrate it easily. The thermos bottle also was cooled to 15°C. A hole was bored through the cork to admit a mercury thermometer which was graduated to degrees only. Subsequent readings were approximated to 1/4 degree. About 15 minutes was consumed in setting up the experiment after lowering the bottle, food, and larvae to 15° C. The readings were made by thrusting the thermometer to about the center of the mass of larvae and food, then raising it to where the mercury could be seen and read. During this fifteen minutes the mass raised its temperature to 18° C. The following is the complete record of the readings:

Table II

Date		Hour	Temperature °C	Date		Hour	Temperature °C
Dec.	15	12:00 M	18	Dec.	20	9:00 a.m.	41
"	"	1:00 p.m.	24	"	"	12:00 M	40.5
"	"	1:30 p.m.	27	"	"	3:00 p.m.	41
"	"	1:45 p.m.	29	"	"	6:00 p.m.	41
"	"	2:00 p.m.	30	"	21	9:00 a.m.	41
"	"	2:30 p.m.	30	"	"	12:00 M	41
"	"	3:00 p.m.	30	"	"	10:00 p.m.	41
"	"	3:30 p.m.	29	"	22	9:00 a.m.	41
"	"	4:00 p.m.	29	"	"	12:00 M	41
"	"	5:00 p.m.	28	"	"	10:00 p.m.	41
"	"	6:00 p.m.	27.5	"	23	9:00 a.m.	40
"	"	7:00 p.m.	35	"	"	12:00 M	40.5
"	"	10:00 p.m.	40	"	"	10:00 p.m.	40
"	16	9:00 a.m.	39.5	"	24	9:00 a.m.	39
"	"	10:00 a.m.	40	"	"	12:00 M	39.5
"	"	11:00 a.m.	41	"	"	10:00 p.m.	39
"	"	12:00 M	41.25	"	25	10:30 a.m.	37
"	"	1:00 p.m.	41.25	"	26	10:00 a.m.	35
"	"	2:00 p.m.	41.25	"	"	7:00 p.m.	34
"	"	5:00 p.m.	41.25	"	27	9:00 a.m.	30
"	"	9:00 p.m.	41	"	"	12:00 M	30
"	"	10:00 p.m.	41	"	"	5:00 p.m.	29
"	17	9:00 a.m.	40.25	"	"	10:00 p.m.	29
"	"	12:00 M	40	"	28	9:00 a.m.	27
"	"	5:00 p.m.	40	"	"	12:00 M	26.5
"	"	9:00 p.m.	40	"	"	10:00 p.m.	26
"	18	9:00 a.m.	40	"	29	9:00 a.m.	25.5
"	"	12:00 M	40	"	"	12:00 M	25.5
"	"	3:00 p.m.	40	"	"	10:00 p.m.	25.5
"	"	5:00 p.m.	40	"	30	9:00 a.m.	25
"	"	9:00 p.m.	40	"	"	12:00 M	25.5
"	19	9:00 a.m.	41	"	"	10:00 p.m.	25.5
"	"	12:00 M	41	"	31	9:00 a.m.	25
"	"	5:00 p.m.	41				
"	"	10:00 p.m.	41.5				

From the above table it will be noticed that at first there was a definitely rapid rise, then a slump and fall of the temperature within the first five hours of the experiment. The rapid rise in temperature is a characteristic of their heat producing ability. The progressive fall between 3 p.m. and 6 p.m. was due to the fact that the bottle was corked up at the beginning of the experiment and by this time the larvae had used up all available oxygen and were suffocating in the bottle. Some of them were lying comatosely on top of the food. At this point the cork stopper was removed and the bottle thoroughly aired by blowing into it from a distance of six or eight inches. From this point on a wire screen was placed over the top of the bottle through which a hole large enough to admit the thermometer was made. It is noticeable that after the means for constant aeration were obtained, the temperature rose to the upper critical level where it stayed fairly constant until December 23. At this point the larvae began to climb up the walls to near the mouth of the bottle and pupate. As a consequence of increasing numbers coming out of the mass and to the quiescent prepupal and pupal stages, the temperature gradually fell to another constant, about 25°C., and this temperature, from 1.5 to 2°C. above the room temperature, was maintained until the imagoes emerged.

Aggregations in Galleria larvae are due to asexually conditioned social tendencies or grouping since sexual relationships obtain only in the imaginal stage. These groupings are due probably to three main causes: (1) their hatching from eggs of the same or related mothers-- The "family origin" (Wheeler '28), (2) their conferring upon each other distinct survival values resulting in social tendencies (Allee '38) and (3) their being positively thermotropistic. This latter might be a result of or cause for (2). It would cause the animals to aggregate in a limited space for their mutual advantage in raising their common temperature. This is evidenced by the fact that if there are 500 to 1000 larvae in combs filling a volume of some 3 cu. ft. the larvae will be found clumped generally near the top strata of combs and occupying a somewhat flattened (horizontally) spherical space of about 2 x 4 inches or a volume of some 35 cu. in. Their locating near the surface instead of deeper in the food mass is not due to the fact that the eggs were deposited there, but probably to their need for air which, of course, would be most accessible near the top. They are also negatively geotropistic and negatively phototropistic which permits their approaching an area near the top surface, yet keeps them sufficiently under it to avoid the light. At night, in the darkened incubator, or when their common temperature has become too high, they may occasionally be found wandering about on the surface; but generally they are burrowing through the mass of combs, webs, and their fellow larvae.

Discussion and Summary

In animal tissues the destructive phase of metabolism (catabolism) is the one most in operation. This oxidizing phase is the animal's only source of energy for its activities or its body heat. Thus the temperature of a living organism under average conditions is always more or less above that of its environment (Starling '20). If the temperature of the contiguous environment were maintained above that of the organism, it would very soon perish. Living tissue, then, maintains a temperature somewhat above that of its environment. The homoiotherms (mammals and birds) maintain temperatures often considerably above their environment. In this case, of course, it is due to the fact that these animals have a two-way regulating mechanism (1) the rate at which heat is produced by their bodies and (2) the rate at which it may be lost. In the lower animals and plants this regulating ability is either very slight or lacking in the individual but may be developed to varying degrees in certain animal societies, groupings or organizations. In cold-blooded animals there is a reduced and variable ability to produce heat and practically no means of controlling its escape from the body.

The aggregating tendency of Galleria larvae coupled both with their rapid growth and constancy of motion (which would be a source for biotic heat) and with the fact that their food stuff and silken webs are excellent insulators against heat loss not only would account for the colonial temperatures but also would be factors of distinct survival value to the species especially for those living in the temperate and sub-frigid zones of the world. The increased temperatures would assure more rapid larval growth and a completion of metamorphosis while its absence would doubtless mean the delay of development and death to great numbers of the species. Moseback and Pukowski ('38) have found in colonies of **Vanessa** larvae a temperature of up to 2°C. above that of their environment. They conclude this is of survival value to the species.

In the case of bees the stimulation for regulatory reactions for the temperature within the hive may be regarded as coming from the temperature outside the hive. While with Galleria the outside temperature seems not to be involved except when it rises to above 40° C. For any temperature conditions below 40° C. the larvae are tending always to raise the temperature of the colony to this upper critical level which perhaps is an optimum for their normal physiological reactions and their development as a whole.

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